THE ROLE OF FIRE REFUGIA IN THE DISTRIBUTION OF *PINUS SABINIANA* (PINACEAE) IN THE SOUTHERN SIERRA NEVADA

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Abstract

Although widespread throughout the interior foothills of central and northern California, *Pinus sabiniana* Dougl. has a disjunct distribution in the southern Sierra Nevada, where it is abundant in the Kern River and Tule River watersheds, but is absent from the Kaweah River watershed between 36° and 37°N. This gap in the pine's distribution has long intrigued botanists and ecologists and has elicited a number of hypotheses for this anomalous biogeographical pattern. Here we propose a new hypothesis that couples unique features of the southern Sierra Nevada topography with unique features of *P. sabiniana*'s response to fire. This low elevation pine is widely distributed in grassland and chaparral, and where it occurs with the latter vegetation, it is extremely vulnerable to high intensity wildfires. Under these conditions, meta-populations persist over time in refugia in riparian areas and during fire-free intervals expand outwards re-colonizing shrubland dominated slopes. The lack of such refugia in the very steep and narrow Kaweah drainage is hypothesized to explain the absence of this pine in that area. To test this hypothesis, we studied the age-structure of *P. sabiniana* in the area of the 2002 McNally Fire in the Kern drainage to compare age distributions of trees and tree skeletons along a gradient up slope away from riparian zones. Maximum age declined significantly with distance from riparian areas, suggesting that past fires have eliminated *P. sabiniana* from the slopes and that the pines have re-colonized during fire-free intervals. The relationship was strongest when our data were restricted to areas that had a previously recorded fire. We also found that the riparian areas in the Kern drainage were significantly wider than those in Kaweah drainage, suggesting that fewer such fire refugia exist in the latter watershed, and providing an explanation for the lack of *P. sabiniana* between 36° and 37°.

Key Words: chaparral, digger pine, fire severity, foothill pine, gray pine, Kaweah, Kern, meta-populations.

The California endemic *Pinus sabiniana* Dougl. (Pinaceae) is a conspicuous tree in the semi-arid foothills of the ranges ringing California's Great Central Valley. This species often occurs in open stands in association with chaparral and wood-lands between 150 and 1200 m elevation (Sud-worth 1908), with a lower elevation limit somewhat higher (300 m) in the southern portion of its range.

A strange feature of *P. sabiniana*'s distribution is a 90 km north-south gap in the southern Sierra Nevada foothills (Fig. 1). For no easily explain-able reason, *P. sabiniana* is absent between the Kings River, Fresno County and the South Fork of the Tule River, Tulare County despite the existence of seemingly suitable habitat. This peculiar gap was commented on by Josiah D. Whitney in 1865 (cited in Griffin and Critchfield 1972) and has been noted by many other authors (e.g., Jepson 1910; Graves 1932; Ledig 1999; Brake 2005). Ledig (1999) has argued that this gap in *P. sabiniana*'s range results from late Pleistocene–early Holocene lakes blocking the pine's dispersal as it migrated into the Great Valley from the Transverse Ranges of southern California. This model depends upon the Pleis-tocene Tulare Lake being a sufficient barrier to

prevent dispersal across the lake and leaves unexplained why there was a lack of northward migration in the foothills between the Kaweah and Tule drainages. Although *P. sabiniana* has a relatively limited mean dispersal distance (Johnson et al. 2003), which might be important on short time scales, rare dispersal events (such as seed dispersal by jays) might be expected to overcome these barriers on longer time scales, as has been documented for some pines (Vander Wall and Balda 1977). Recently, Brake (2005) proposed an alternative explanation for this distribution gap, which was that increased species diversity in the area of the gap has competitively excluded *P. sabiniana* from this region.

Graves (1932) proposed that this distribution gap between the Kings and the S. Fork of the Tule rivers could be explained on the basis of fire. His hypothesis was that some large historical fire or fires had extirpated *P. sabiniana*, but it did not explain why the gap should be in this particular region. Also addressing this range discontinuity, Watts (1959) suggested that Native American burning in the Kaweah may have resulted in large fires that excluded *P. sabiniana*.

Fire is an important part of *P. sabiniana*'s ecosystem as well as for the majority of pine
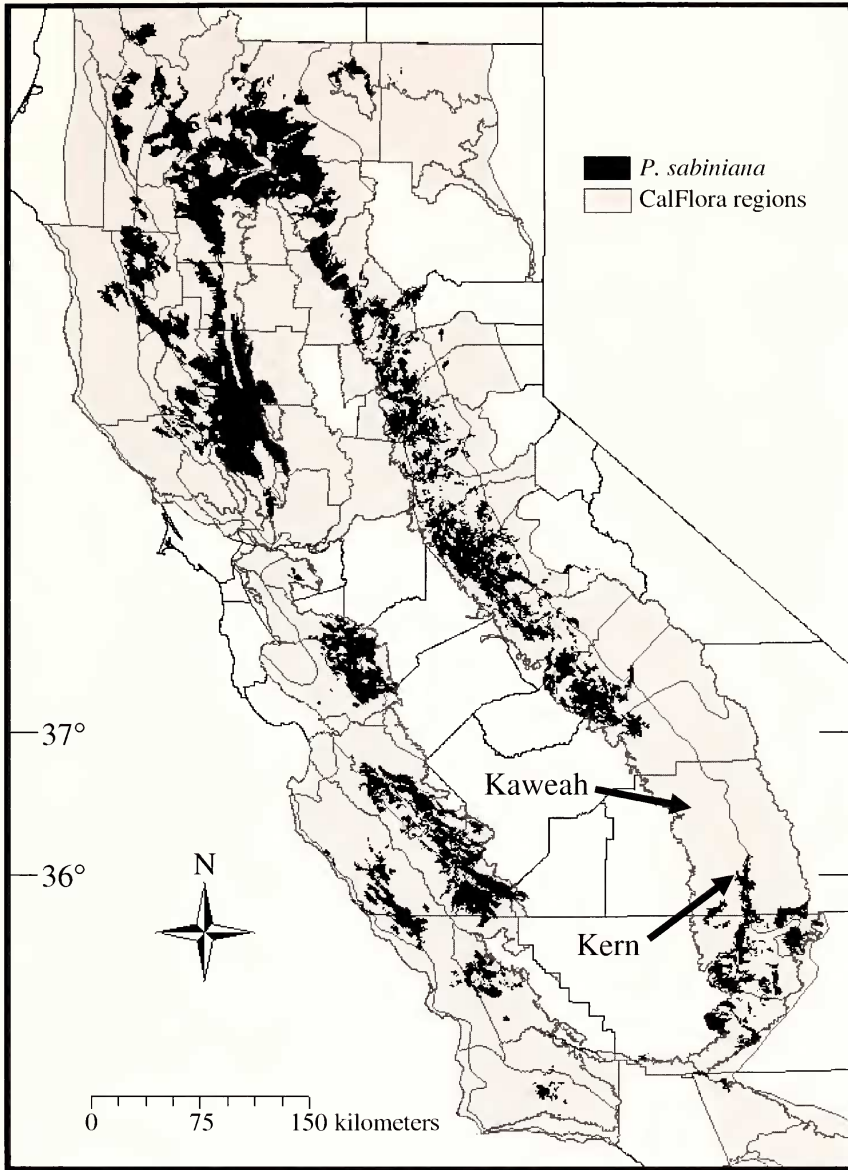
FIG. 1. *Pinus sabiniana* distribution (shown in black) in California according to the GAP Analysis Project (USGS 2006). The Jepson/CalFlora regions where *P. sabiniana* may be expected to occur are shown in gray (Hickman 1993), however, this pine is absent from the Southern Sierra Nevada between 36° and 37°N, which includes the Kaweah watershed indicated on the map. Also, indicated is the Kern drainage where the field study was conducted. Other areas mentioned in the text include the Kings River to the north of the Kaweah and the Tule River west of the Kern.

species. Pines in fire-prone regions fall generally into one of two groups: those in surface-fire regimes that survive fire through thick bark, greater mature height, and self-pruning of dead branches, and those in crown-fire regimes that have more flammable architectures and are easily killed by fire, but have serotinous cones that cue seedling establishment to take advantage of extensive fire-cleared gaps (Keeley and Zedler 1998). Schwilk and Ackerly (2001) have placed these strategies into an evolutionary

context and argued that they have resulted from a repeated pattern of correlated evolution between the "fire-surviving" and the "fire-embracing" strategies that comprise suites of structural and life-history traits. Although these patterns appear to hold up for most pines, and over widely separate parts of North America, three low elevation California pines, *P. sabiniana*, *P. coulteri* D. Don, and *P. torreyana* Carrière, appear somewhat anomalous (Keeley and Zedler 1998). *Pinus sabiniana* has traits such as thick

bark (Johnson et al. 2003) similar to the "fire surviving" pines, but does not self-prune dead branches and does not typically survive fire (Graves 1932; Lawrence 1966; Borchert et al. 2002). Furthermore, *P. sabiniana* has cones that are generally not serotinous, although (Johnson et al. 2003) have argued that seeds cached in the soil by animals provide an alternative local dispersal mechanism in place of serotiny for *P. sabiniana* and its close relatives *P. coulteri* and *P. torreyana*.

Largely unexplored to date is the possibility that there are unique attributes of the Kaweah watershed that may explain the gap in *P. sabiniana* distribution. This is a region of anomalous topography: The transition from the Great Valley to the Sierra Nevada is steeper and more abrupt here than it is north or south of this area. Saleeby and Foster (2004) argue that the area between 36° and 37°N (which corresponds nearly exactly to the gap in the *P. sabiniana* distribution) represents a region of convective mantle "drip" centered west of the Sierra Nevada: subsidence results in the steeply faceted mountainous topography here actively being buried under the sediments of the Great Valley. Comparing sites within the gap to sites north and south of the gap, Brake (2005) found that the sites in the distribution gap had increased slope and more exposed rock.

While we doubt that steep terrain alone can explain the lack of *P. sabiniana* in this region, we believe that when coupled with the following observations on fire response, it may indeed contribute to the absence of this pine in the Kaweah drainage. South of the Kaweah watershed there are extensive stands along the Kern River and its tributaries north of Kernville. Much of the middle and lower Kern watershed burned in the McNally Fire during July, 2002. Because this low elevation pine is commonly interspersed in chaparral shrublands, fires are typically large and of high intensity. After the fire, we observed that many thousands of pines were killed and pines survived primarily in the broad alluvial areas that parallel watercourses (Fig. 2). Most trees outside of these river valleys were killed and very little seedling recruitment was observed in the area of the McNally burn (Keeley et al. 2005).

In light of these observations, we propose a new model for pines in fire prone habitats that differs from the fire embracing and fire surviving models of pine-fire coexistence. This is the fire refugia model and it is offered as an explanation for both the long term persistence of *P. sabiniana* in landscapes such as the Kern that are periodically subjected to high intensity crown fires and explains the biogeographical gap in its distribution centered on the Kaweah watershed. We hypothesize that periodic high intensity fires eliminate *P. sabiniana* from many upland sites and that meta-populations survive such events by persistence in refugia in the bottoms of ravines and alluvial plains. During the intervals between fires pines re-colonize slopes and persist until the next high intensity fire. Thus, we imagine the population dynamics of this pine to be one of periodic fire-induced contraction and expansion. This hypothesis is similar to the model proposed by (Zedler 1981) for closed-cone cypress, and to that suggested by (Keeley 2006) for big-cone Douglas fir in the Transverse Ranges of southern California. We suggest that the distribution gap in the Kaweah watershed results from it being a region of steeper topography that lacks broad, riparian refugia.

The purpose of the present study was to test this fire refugia hypothesis by investigating patterns of pine distribution in the 2002 McNally Fire. We predicted that if *P. sabiniana* must re-colonize hillsides from refugia, then we should see a shift in pine age structure along a gradient from the valley bottoms up the slopes, with tree age declining along the gradient. In addition, we investigated our biogeographical gap hypothesis by testing the prediction that the width of potential riparian refugia would be smaller in the Kaweah drainage than in the Kern.

Methods

The McNally Fire burned 25,100 ha of the lower Kern watershed of Sequoia National Forest during July 2002. We randomly selected seven transects within the area burned by the McNally Fire, with the requirement that each of the four accessible main drainages within the burn that contained *P. sabiniana* habitat were represented by at least one transect. These drainages were the Kern below the confluence with Brush Creek, Brush Creek, South Creek, and the North Fork of the Kern above the confluence with South Creek. Transects were positioned by selecting a random point along the bottom of the drainage within a pre-selected section several km long and placing the transect directly parallel with the fall line at that point. Transects were 50 m wide and 500 m long. Transects began at the watercourse in the valley bottom and proceeded directly perpendicular to the lower slope contour. This resulted in transects that generally increased in altitude, but occasionally crested side ridge lines and descended slightly near the end.

Within each transect, every *P. sabiniana* individual (alive or dead) was recorded and its position marked with a GPS unit. The diameter at 50 cm height was measured on each tree. To determine a diameter-age relationship, we cut slabs for counting rings from 29 trees over a wide a range of diameters. For aging, we attempted to distribute our sampling over a range of eleva-

FIG. 2.   Example of a *P. sabiniana* stand in an alluvial corridor that survived the 2002 McNally Fire in the Kern watershed, whereas all pines on the slopes above were killed.

tions, but for larger trees that would be dangerous to fell, we were limited to trees already felled after the fire by the USDA Forest Service as hazard snags along the roads and near campgrounds. We aged trees that fell outside the transects as well as those inside to increase

our sample range. It was possible to cross-date approximately one third of the trees by matching narrow rings with known drought years in this region (drought years supplied by Tony Caprio, NPS, Sequoia-Kings Canyon).

Our hypothesis predicts that maximum tree age should decrease with distance from the putative refugia in the riparian zone. In other words, we should expect young and old trees low in the transect, but only young trees high in the transect. To test this, we used quantile regression on age versus distance. We wish to test how the maximum tree age changes with distance and quantile regression is useful for cases such as this where we are interested in how the extreme changes, rather than the mean (Koenker and Bassett 1978). We explored quantiles (τ) of 0.85, 0.90 and 0.95. All statistical analyses were conducted with the R statistical language (R Development Core Team 2005). The R quantreg module was used for quantile regression. Using fire-history data maintained by the U.S. Forest Service since 1910, we categorized our transects into two groups: those that had experienced a previous fire and those that had no recorded fire history prior to the 2002 burn. One transect had burned in 1934 and two had burned in the same fire in 1940. In the areas with no previously recorded fires, we cut stem sections from standing skeletons of non sprouting *Arctostaphylos viscida* C. Parry. Although the center of the stems were often rotted, we counted 107–127 rings in individuals at two locations and estimated ages of between 130 and 150 yr (unpublished data, Keeley et al. 2005).

To test our hypothesis that the Kaweah watershed may provide fewer fire refugia than the Kern, we compared the topography of the two watersheds. We characterized the distribution of slopes within each watershed between 300 and 1800 m using a geographic information system (ARCGIS, ESRI) and USGS digital elevation data to test for a difference in overall steepness, which may influence fire intensity. To test for differences in the distribution of potential riparian/alluvial refugia, we measured the average width of riparian areas in six stream/river drainages in each watershed, with two to three measurements at random points along each stream. We defined this width as the distance between opposite slopes containing a stream drainage in which the slope was less than 30 degrees. The drainages were selected at random among a set of 10–15 potential drainages per watershed. These widths were calculated using the USGS 7.5 min maps.

RESULTS

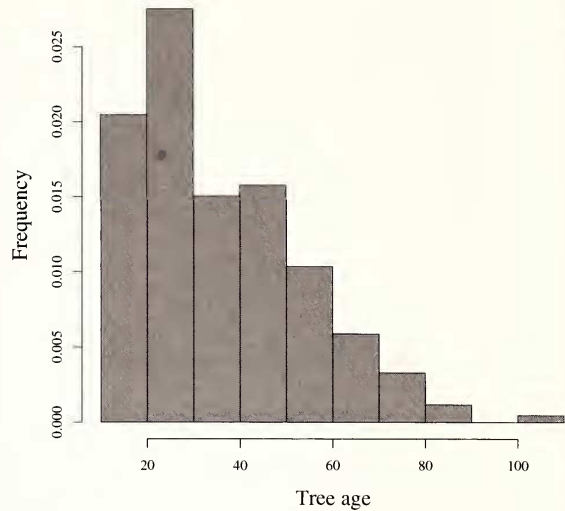We counted rings on 29 trees to develop a dia-meter-age prediction equation. The approximate

FIG. 3. Predicted age distribution for all *P. sabiniana* using pooled data for seven transects (N = 425), where age = 0.7766 × basal diameter + 14.28.

ages ranged from 9 to 112 yr (8–113.5 cm). A linear regression described the relationship between basal diameter and age ($F_{1,26} = 121.9$, $P < 0.001$, $r^2 = 0.82$). We predicted age for all trees according to the resulting equation: age = 0.7766 × diameter + 14.28. Predicted ages ranged from 14 to 101 yr (Fig. 3). We divided our aged trees into two samples, slope and valley stream bottom to test for a different diameter-age relationship depending upon location, but found no evidence for such a difference. We therefore used the overall regression to predict ages.

Transects began in the level riparian/alluvial areas and left the stream alluvial area within 10–50 m. The hill slopes themselves varied from 15–30° in steepness. Quantile regression on predicted age as a function of distance from the base of the transect resulted in negative regression slopes for each of the 7 transects. A single sample t-test on these slope values indicated that the mean slope (-0.05) was significantly different from zero (t = -3.94 df = 6, P = 0.007). Figs. 4 and 5 show the age/distance results for all seven transects.

Using fire-history information maintained by the U.S. Forest Service, we categorized transects into those that had experienced a fire previous to the 2002 burn (Fig. 4) and those that had no recorded fire (Fig. 5). The mean quantile regression slope for transects in areas that burned previously was significantly lower (more negative) than the mean slope for areas that had not experienced a previous fire (means = -0.073 and -0.018, Kruskal-Wallis $\chi^2 = 4.5$, P = 0.034). These results were consistent across several values of τ (Table 1).

Although all transects had burned in the 2002 McNally Fire, some trees survived even this very intense fire. Logistic regression on the probability
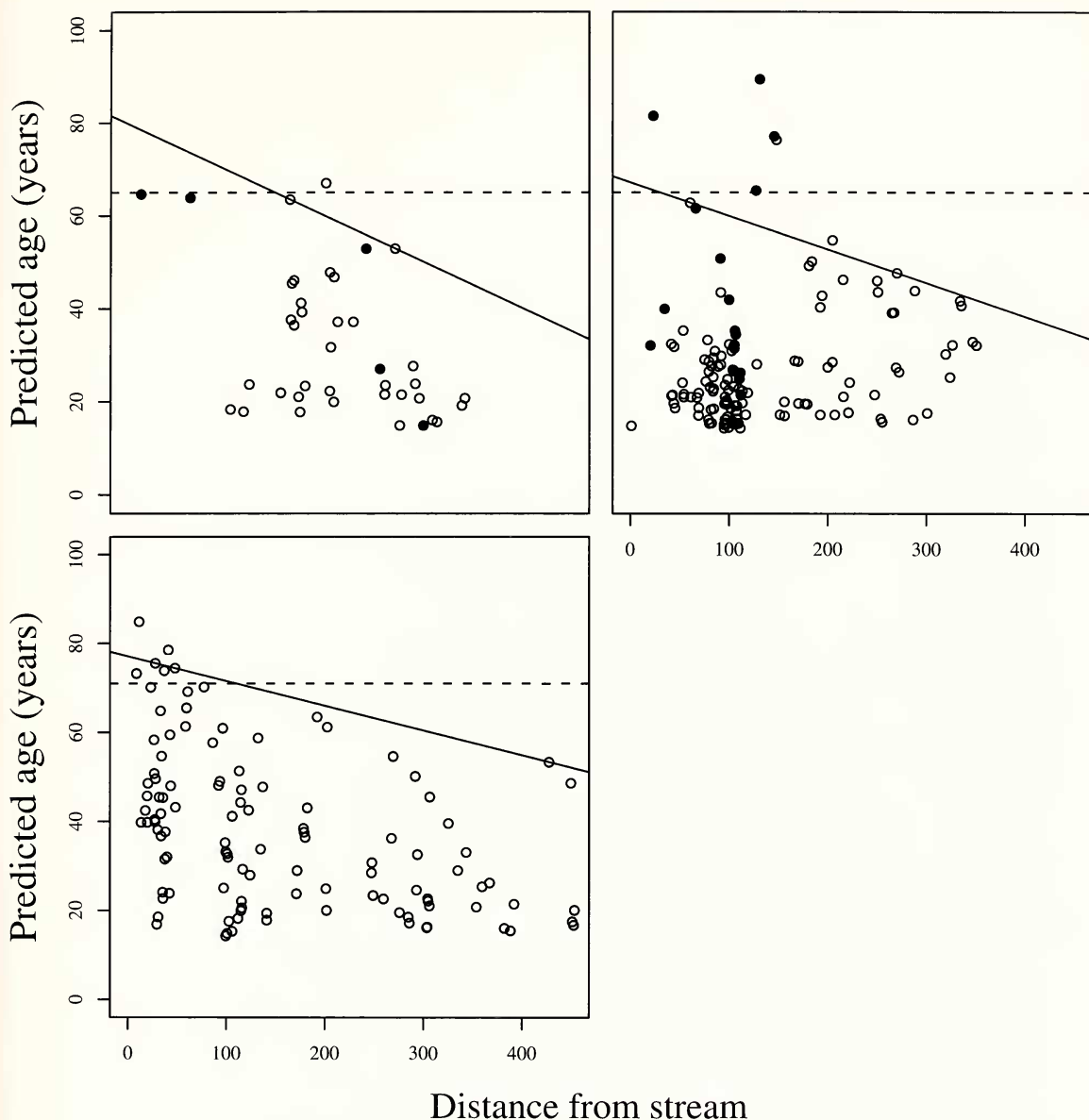
Fig. 4. Age vs distance relationship for the three transects that occurred within the boundaries of a recorded fire prior to the 2002 McNally Fire. Solid circles show trees that were alive following the McNally fire; open circles show dead trees. Solid lines show the $\tau = 0.95$ quantile regression. The mean quantile regression slope was -0.018. The dashed lines indicate the time of the last recorded fire prior to the McNally burn.

of tree mortality reveals that distance from the valley bottom significantly increased mortality (model: likelihood of survival = distance + transect, Wald $Z = -4.22$, $P < 0.001$). The mean distance for living trees was 126.1 m and the mean distance for dead trees was 170.3 m.

Mean slopes within *P. sabiniana's* elevational range did not differ significantly between the Kern and Kaweah watersheds nor did the proportion of very flat terrain (slope < 5°): the proportion was approximately 6% for both watersheds. This measurement does not distinguish between valleys and plateaus, so we also

investigated valley widths, which may better correspond to fire refugia. However, the average width of riparian/alluvial valleys did differ significantly between the two watersheds. The average width in the Kern was 177 m ($\tau = 138$) and in the Kaweah it was 79 m ($\tau = 41$) (t-test, N = 32, p = 0.013).

DISCUSSION

Our study supports the hypothesis that *P. sabiniana* in the Kern watershed must re-invade the slopes after being eliminated by severe
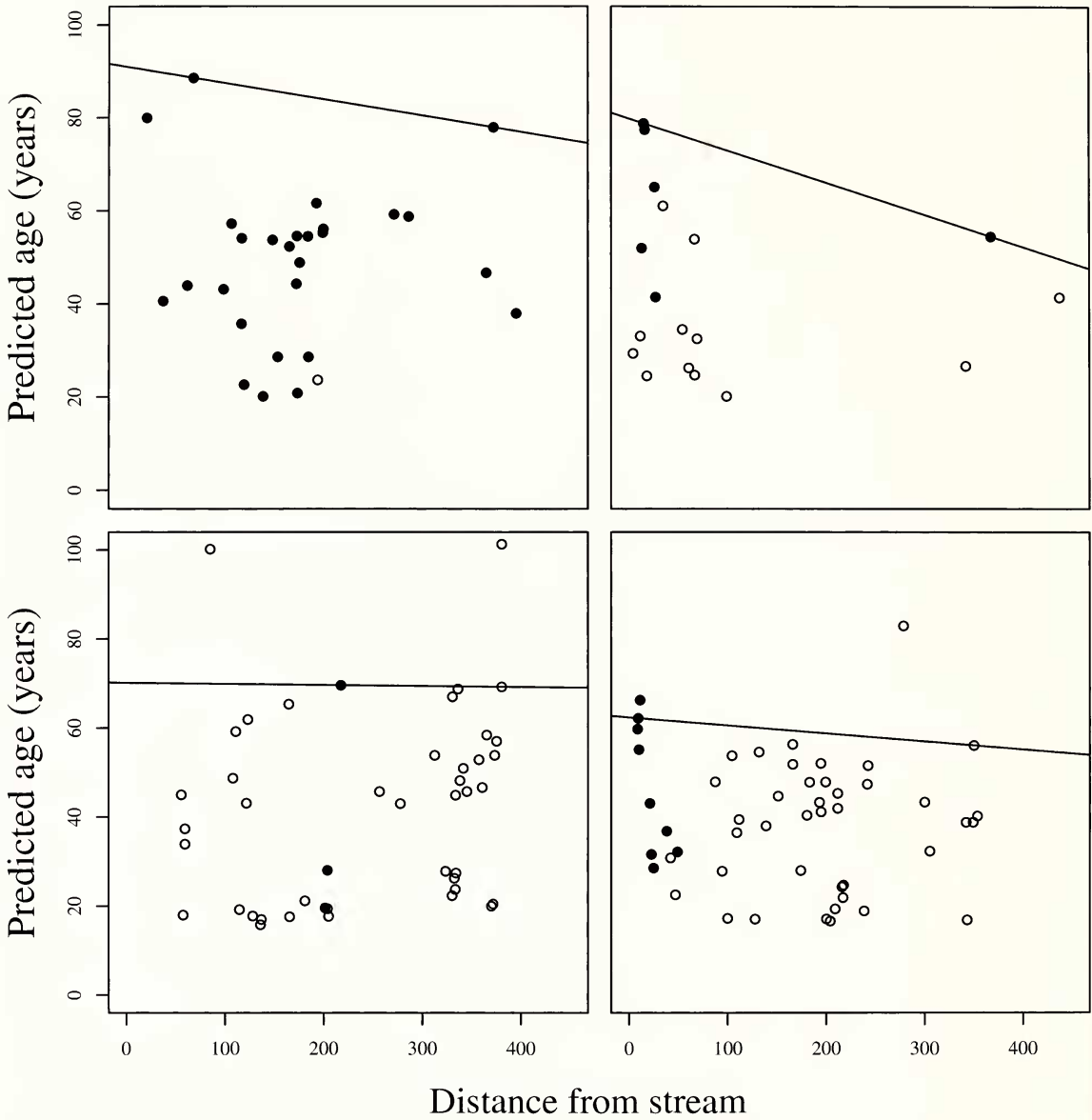
FIG. 5. Age vs distance relationship for the four transects that had no recorded fire prior to the 2002 McNally Fire. Solid circles show trees that were alive following the McNally Fire and open circles show dead trees. Lines show the τ=0.95 quantile regression. The mean quantile regression slope was −0.073.

wildfire. The decrease in upper quantile tree age with distance from the stream or valley bottom is consistent with the hypothesis that this re-colonization from valley bottom fire refugia is a gradual process. Many chaparral plants that are killed by fire have a soil-stored seed-bank and fire-cued germination that allows for rapid population recovery following fire. In contrast,

TABLE 1.   QUANTILE REGRESSION SLOPE ESTIMATES AND 0.95 CONFIDENCE INTERVALS ON SLOPES FOR THREE VALUES OF τ. Data from all transects were pooled into the two categories according to past fire history prior to the McNally Fire.

	τ = 0.85			τ = 0.90			τ = 0.95		
	slope	conf. bounds.		slope	conf. bounds		slope	conf. bounds	
Recorded fire	−0.056	−0.101	−0.014	−0.059	−0.093	−0.033	−0.058	−0.090	−0.043
No recorded fire	−0.009	−0.029	0.035	0.001	−0.052	0.022	−0.026	−0.033	0.033

recovery by *P. sabiniana* appears to be much slower. We estimated ages of non-sprouting *Arctostaphylos viscida* at 130–150 yr those sites with no previous recorded fire. *P. sabiniana* individuals near these *Arctostaphylos* were much younger (20–30 yr), indicating that the pines had recruited years after the last fire prior to the McNally Fire. In fact, the maximum age of *P. sabiniana* sampled in this study was approximately 100 yr (Fig. 3). Thus, it is apparent that in a chaparral dominated landscape, which experiences recurring intense fires, this tree is dependent upon fire refugia for long term persistence. As a result, this pine exhibits population fluctuations quite unlike those of other pine strategies. For example, the fire-surviving strategy of ponderosa pine results in only small localized gaps that are rapidly re-populated from parent trees surrounding the gaps. The fire-embracing strategy of knobcone pine results in total population annihilation but regeneration in situ from a serotinous seed bank. This third model of pine life history depends on meta-populations, whereby populations shrink and persist in refugia, but expand outwards during fire-free intervals.

Short-range dispersal in *P. sabiniana* may act to maintain the age-distribution gradient. *P. sabiniana* seeds have an extremely reduced wing and are not dispersed easily by wind, but appear dependent upon animal seed dispersal (Keeley and Zedler 1998; Johnson et al. 2003). Investigation of the closely related *P. coulteri* has shown that seeds are dispersed by scatter-hoarding rodents close to the parent tree with a mean distance of 15.3 m (Borchert et al. 2003). *P. sabiniana* reaches maturity at 10–20 yr (Krugman and Jenkinson 1974), although seeds on trees as young as two years have been recorded (Watts 1959). Limited dispersal and a moderate age to reproduction seem to combine to slow the advance of this tree into burned areas.

Since our data from the Kern watershed shows that *P. sabiniana* depends upon fire-protected refugia, a lack of such refugia in the region of the distribution gap may explain the discontinuity in the species's range. The difference in mean valley widths between the Kern and the Kaweah watersheds does indicate that the Kern may provide better fire refugia than does the Kaweah, and therefore a higher probability of long-term population persistence. In addition, although our comparison of mean slopes according to digital elevation models did not detect a statistically significant difference in average steepness between the Kaweah and the Kern, previous work by (Brake 2005), did find significantly steeper slopes in the gap than at similar elevation sites to the north and south.

However, riparian areas and alluvial plains are not the only potential fire refugia for pines.

Rocky outcrops on slopes allowed some pines in the Kern to survive the McNally Fire and there are some rock outcrops in the Kaweah drainage. Although we have not investigated this closely, it appears from our observations that the combination of steep terrain and dense vegetation of the Kaweah may readily carry fire into such rock outcrops, thus diminishing their value as refugia. Although fire refugia appear to be important to *P. sabiniana* in the southern Sierra Nevada, this pattern of stand-replacing fires restricting populations to refugia may not apply across *P. sabiniana's* entire range. In areas were the pine grows within a matrix of grassland, it may not be subject to the same stand-replacing fires it experiences in the Kern where it grows among chaparral. Knowledge of the fire-response and age structure throughout *P. sabiniana's* range, as well as the degree of variation in cone and bark traits within the species, would help us better understand the life history and biogeography of this pine.

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